[thesis, University of Wyoming (1962)]. Dolomite occurs in secondary cave deposits in Carlsbad Caverns, New Mexico, where it is believed to be altered from aragonite by reaction with magnesium-rich solutions [J. Thrailkill, *J. Sedimentary Petrol.* **38**, 141 (1968)].

44. Shelta Cave, Huntsville, Alabama, is being purchased by the National Speleological Society because of the very large diversity of troglobites and the presence of a unique shrimp and crayfish. Ezell's Cave in Texas is being purchased by Nature Conservancy because it contains a rare and unique troglobitic salamander, *Eurycea rathbuni*, as well as relict species of flatworm, amphipod, and shrimp. The possibility of declaring the Flint Ridge Cave System in Mammoth Cave National Park, Kentucky, an underground wilderness under the Wilderness Act of 1964 is currently a hotly debated topic.

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Vegetational Change Along Altitudinal Gradients

Studies in Ethiopia show that discreteness of zonation varies with steepness of slope.

Edward W. Beals

The controversy among plant ecologists as to whether vegetational variation is predominantly continuous or discontinuous still goes on and occasionally reaches the pages of *Science* (*1*, *2*). The continuum school of thought, originating out of Gleason's individualistic concept of plant associations (*3*) was originally developed in this country during the 1950's by Curtis and his associates (*4*) and by Whittaker (*5*). A parallel development occurred among Polish ecologists (*6*). The other view, illustrated by Clements' organismic concept of the community (*7*) and by the elaborate taxonomy of communities put forward by Braun-Blanquet and his colleagues (*8*), has been staunchly defended by Daubenmire (*1*), who claims that the continuums described by most authors are artifacts of data manipulation.

It may be significant that continuum concepts originated largely among ecologists living in areas of gentle topography—in Poland and in the Midwest. Braun-Blanquet's ideas were formulated largely in mountainous Switzerland, and Daubenmire's experience has been mostly in the western mountains of the United States. Whittaker's gradient analysis in the Great Smoky Mountains (*5*) showed continuity but also some discontinuity in the vegetational changes.

It is apparent to many ecologists that under some conditions vegetation forms a continuum, under other conditions it forms discrete communities, and that most vegetation is somewhere between. The question is, What factors determine the relative continuity of the vegetation? Are there factors operating besides the obvious ones, such as predominance of certain combinations of conditions in an area, or inherent environmental discontinuities, or random fluctuations?

Comparison of the Two Study Areas

Two areas in Ethiopia allow a unique comparison of the effects of steep and gentle altitudinal gradients on vegetational change. One area is located on the Rift Escarpment (11°5′N, 40° to 39°50′E), beginning below the village of Bati and extending westward up to the town of Combolchia. This steep gradient extended from 800 to 2050 meters (a vertical change of 1250 meters) in about 20 kilometers horizontal, and the topography was rugged. The other area is in the Rift Valley (9°N, 40°10′E to 7°15′N, 38°35′E), from Awash Station southwest to Shashamanne. This gentle gradient extends from 1000 to 1900 meters (a vertical change of 900 meters) in about 300 kilometers horizontal, and the landscape, except for a few isolated volcanic peaks, is gently rolling to flat. Though this gradient has less altitudinal range than the other one, its greater geographic range is compensatory, and the vegetational types in the two areas are somewhat similar. The two areas are within 235 kilometers of each other.

One environmental difference, resulting from contrasting topography and causing considerable difference in the vegetation, is the depth and stability of the soil—in the former case shallow, rocky, and poorly developed; in the latter case relatively deep and well developed. The soils throughout both areas of sampling are derived from basic volcanic rock.

Moisture is probably the overriding factor influencing altitudinal zonation. Neither area receives frost. *Acacia* scrub communities occur at lower elevations.

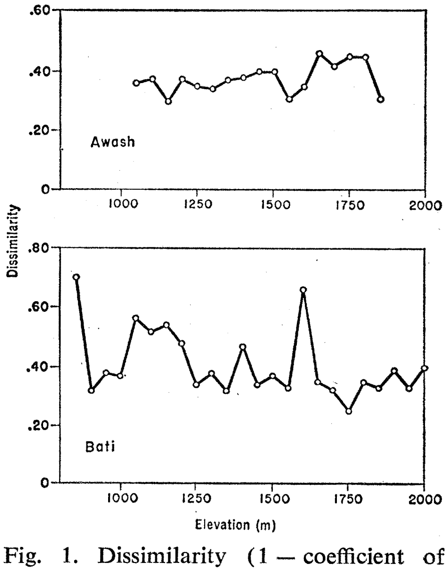

Fig. 1. Dissimilarity (1 — coefficient of similarity) of adjacent segments of the altitudinal gradient along the gentle (Awash) and the steep (Bati) slopes. High values indicate rapid changes in vegetation, low values indicate slow changes.

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Acacia nubica is more common on the gentle gradient, and *Acacia flava* is found only there. *Acacia mellifera* is more common on the steep gradient, and *Acacia venosa* is found only there. Above these *Acacia* scrub communities is a band of tall *Acacia senegal* scrub on both gradients. The next zone of vegetation is rather broad in both areas, but it differs in character in the two areas. Along the steep gradient it consists of tall *Acacia asak* scrub, while along the gentle gradient it consists of *Acacia tortilis* woodland. Above these zones, there is a zone of *Euphorbia candelabrum* woodland. The *Acacia asak* zone of the steep gradient passes directly into the *Euphorbia* zone, whereas on the gentle gradient, there is a *Euphorbia–Acacia etbaica* woodland before the zone of pure *Euphorbia.*

Fieldwork was carried out in 1963 and 1964. Vegetation was sampled at approximately 10-meter altitudinal intervals in both areas, determined from altimeter readings corrected for temperature and for the regular daily fluctuations of pressure characteristic in the tropics. Because each new sample was related to the one below it at about the same time, relative altitudinal values were reasonably accurate. Sample areas along the steep gradient were all facing east, east-northeast, or east-southeast. Those along the gentle gradient were nearly level; none were selected which had detectable west or south slope.

A sample consisted of ten plots each 20 by 10 meters (the total area sampled was 0.2 hectare). The plots were laid end-to-end as nearly as possible and followed the contour of the land. All woody plants over 1 meter tall were recorded. For this analysis, the altitudinal gradient in both areas was divided into segments of five combined samples, each segment representing 50 meters of elevation. The coefficient of similarity used for comparison between adjacent segments was $S = 2w/(a + b)$ (*9*), where w is the sum of species densities which the two segments have in common, and a and b are the sums of species densities of the two respective segments. The coefficient ranges from 0, if two segments have no species in common, to 1 (100 percent) should they have the same density of the same species. Over 100 species of woody plants were used to obtain similarity values in both areas.

The mean coefficient of similarity for both areas was remarkably similar (Bati, 59.1 percent; Awash, 62.5 percent), but the distribution of coefficients was quite different—symmetrical and apparently normal for the gentle Awash gradient, highly skewed for the steep Bati gradient (Fig. 1). The variance ratio ($F = 5.85$) showed that the variances of the two slopes were significantly different ($P < .001$). A chi-square test was applied to the coefficients in each area, testing the observed w values against the w values expected on the basis of the mean coefficient. Along the gentle slope, χ^2 was 7.8 (d.f. = 16, $P > .95$), suggesting significant uniformity in rate of change. Along the steep slope, χ^2 was 56.6 (d.f. = 23, $P < .001$), indicating highly significant irregularity in the coefficients. The peaks along the steep Bati slope (Fig. 1) represent significantly more rapid vegetational change than the broader depressions, and indicate more marked zonation along the slope than along the gentle Awash slope.

Because the two gradients were sampled at regular altitudinal intervals, random fluctuations of the data are reduced, and clustering of stands due to their predominance at certain altitudes is eliminated. Furthermore, the method eliminates obvious differences in distinctness of zonation between steep and gentle slopes, which are caused simply by the difference in rate of environmental change over the same distance.

The distributions of species along the altitudinal gradients (Fig. 2) show marked differences in the two areas. In some cases, comparisons of the same

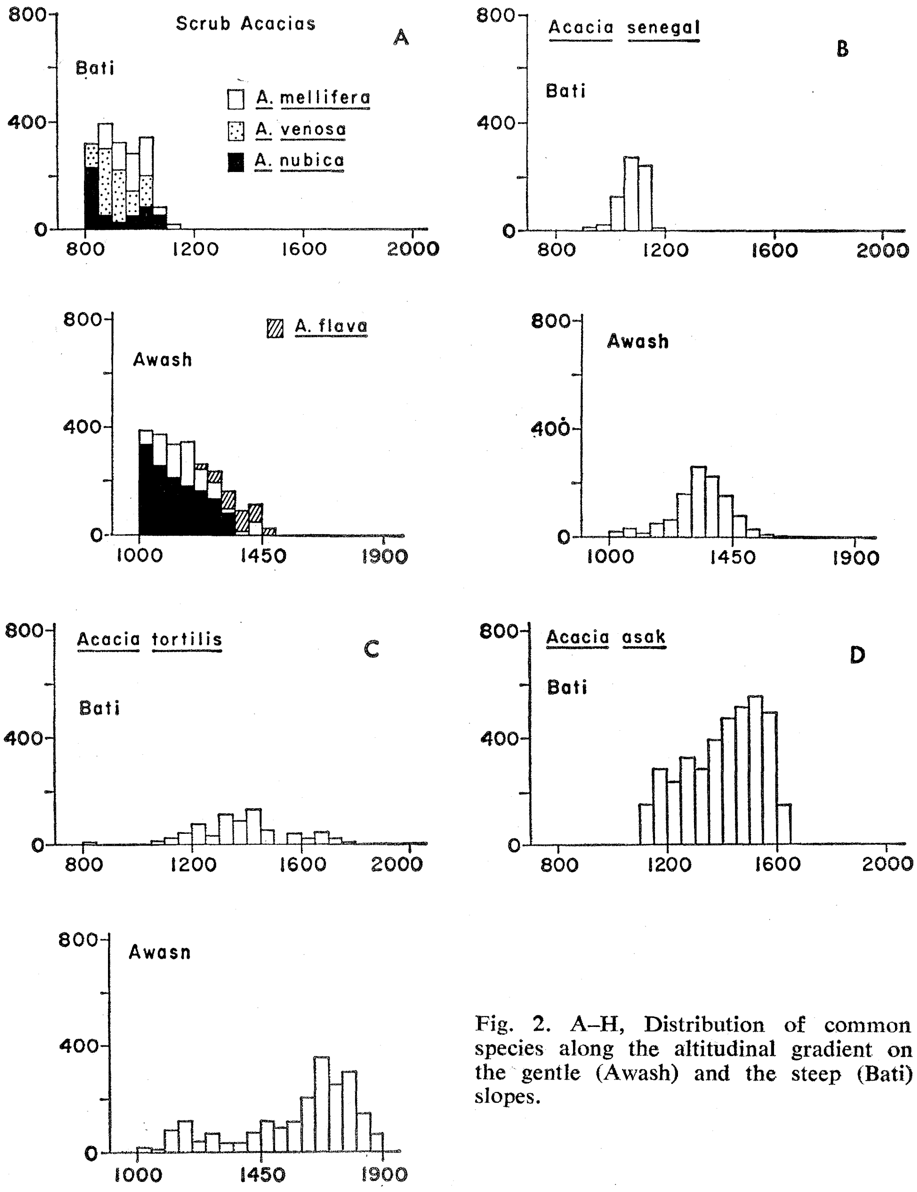


Fig. 2. A–H, Distribution of common species along the altitudinal gradient on the gentle (Awash) and the steep (Bati) slopes.

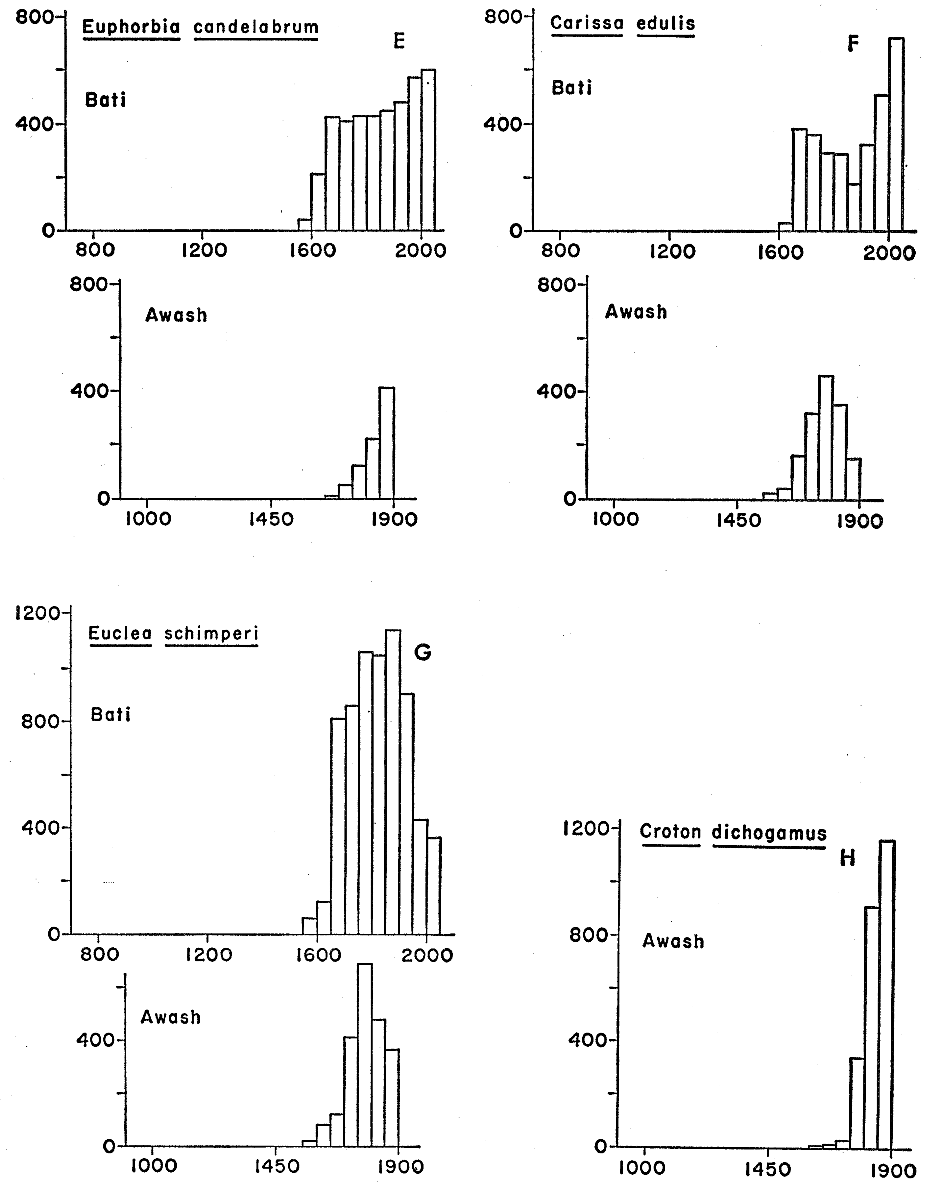
species in the two areas can be made; in other cases, the comparisons must be between different but ecologically comparable dominants. There is a distinct trend toward more sudden appearance and disappearance of species along the steep gradient (Bati) than along the gentle one (Awash).

Whittaker (*5*) demonstrated plateau-type distributions in the Great Smoky Mountains. He postulated a normal curve truncated by the maximum density possible in the habitat. This could explain in part the distributions of the *Acacia* scrub and of the *Euphorbia*. However, the more striking aspect of distribution on the escarpment is the steep slopes rather than the flat tops. There may be factors brought about by the steep altitudinal gradient which cut off the tails of a bell-shaped curve.

Role of Competition

Competition is a possible factor contributing to the sudden changes from rarity to commonness along the steep gradient. Hutchinson (*10*) explains discrete ecological zonation along a continuous physicochemical gradient (particularly as it relates to a freshwater-marine sequence) in terms of the principle of competitive exclusion (*11*). When two species, ecologically similar except for one factor, are grown along a gradient of that factor, there will be a definite point along the gradient below which one species will succeed to the exclusion of the other, above which the other species will succeed to the exclusion of the first (*10*).

Gause and Witt (*12*) constructed a theoretical model for two competing species along a temperature gradient, and they concluded that because of changes in competition, "under the influence of temperature (and any other) gradient a mixed population separates into a number of distinct types."



Plants have attributes that make the role of competition somewhat different from the role of competition among animals. First, plant propagules are dispersed passively, and their settling in a favorable environment is usually a matter of chance. Second, once a seed germinates, the resulting plant is permanently attached to that spot. Third, because of its immobility, the plant will cause important but local changes in the physical environment. For these and other reasons, the spatial distribution of both seeds and plants is all-important in considering the role of competition.

Skellam (*13*) has shown that, with a random distribution of seeds of two species, there may be areas in the landscape where each species can grow without competition from the other. Only when seed density of one species is very high will the empty areas of a random pattern be so small as to preclude noncompetition between species. As Cole (*14*) has pointed out, a nonrandom aggregated distribution of seeds, which may be more common in nature than random, will increase the areas of noncompetition. The two species may therefore coexist in an equilibrium which is dependent on such factors as the number of seeds produced by each, their relative success where the two do occur together, their density, and their spatial pattern. The overwhelming evidence that stable plant communities often do form a continuum (*15*) suggests that Skellam's models may frequently be a closer approximation of the realities of vegetational distribution than are competitive-exclusion models.

Two species occupying more or less comparable habitats at different altitudes, however, may very well be in greater competition in their zone of contact if the altitudinal gradient is steep. Dispersal into the marginal habitat of both species will be greater than it will be along the gentle gradient, because the optimum environment for the species will be nearer. When two competing species have high reproductive potential in the same area, then slight differences along the environmental gradient may indeed make a big difference in which one fails and which one succeeds.

It was possible to compare interactions of two species under conditions of dominance and of subdominance. The two species were leguminous shrubs, *Cadia purpurea* at lower elevations and *Calpurnia subdecandra* at higher elevations. In the Bati-Combolchia region the two species are common but not dominant components of the shrub layer. About 100 kilometers north of Bati, below the town of Corbetta, is a similarly steep gradient, which had been burnt-over several years previously. These two species recovered after fire much better than other species and have become dominant in this area. This steep gradient was sampled from 1900 to 2500 meters in the same way the other gradients were.

Where *Cadia* and *Calpurnia* are not dominant, they show nearly normal distributions and overlap considerably; where they are dominant, the two species show flat-topped, nearly tailless distributions and overlap very little (Fig. 3). The enhancement of abrupt distributions by dominance suggests that competition is important.

Influence of Other Factors

The role of vegetative reproduction in causing abrupt distributions is obvious and has been documented in at least one vegetational type (*16*). Both *Cadia* and *Calpurnia* may spread vegetatively, and the striking discontinuity along the Corbetta slope (Fig. 3) is possibly enhanced by this fact. But it is unlikely that this would be responsible for the differences between slopes, and many other species which show this peculiar pattern of distribution do not regularly reproduce vegetatively.

Variation in the climate may also affect continuity. A more stable climate might produce sharper ecotones (assuming that "typal communities" do exist), while an extremely variable climate might produce very broad ecotones which could mask the "typal communities." Rainfall and temperature records were examined from two weather stations along the steep slope—Bati and Combolchia—and for three stations along the gentle slope—Awash, Adama, and Shashamanne. Records from the steep slope generally had a higher variance in annual rainfall, August rainfall, January mean temperature, and July mean temperature. These differences suggest that the more continuous vegetational gradient may actually have had the more stable climate. However, variance-ratio (*F*) tests of the two *Acacia*-scrub stations, Bati and Awash, and of the two *Euphorbia* woodland stations, Combolchia and Shashamanne, revealed no significant difference in variance (possibly because of the shortness of records, 5 to 10 years). Climatic variance has apparently not been important in causing the differences in zonation of the two areas. It may have prevented the boundaries between zones of the steep slope from being even more distinct.

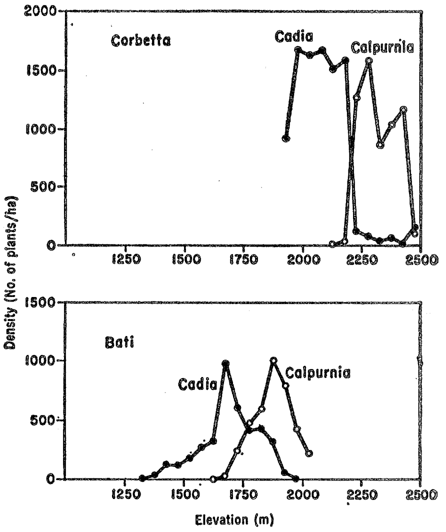


Fig. 3. Distribution of two species along a steep altitudinal gradient where they were dominants (Corbetta slope) and where they were subdominants (Bati slope).

Discontinuities in the substrate would be important, but only one instance of a sharp discontinuity was detected on the Bati slope—the rapid change in vegetation at the bottom of the slope was caused by the parent material of the two lowest samples (dominated by *Acacia nubica*) being talus, that of all other samples being bedrock. The entire escarpment in this region is covered by volcanic basalts of similar age and composition. Differences in several soil and topographic factors were tested among the three major altitudinal zones, and some significant differences were detected: the lowest zone exhibited less degree of slope, shallower soil, and fewer samples with east-southeast slopes (as opposed to east-northeast and east) on the average than did the other zones; there was an increase in soil organic matter, soil acidity, and changes in soil nutrients, with increasing altitude. However, none of these factors exhibited marked discontinuities. Tests of the difference in these factors between adjacent segments of the altitudinal gradient showed that those pairs of segments with dissimilarity greater than .45 had no greater environmental differences than did those pairs with dissimilarity less than .45. Thus, no environmental discontinuity was detected along the steep gradient, except for the talus-bedrock transition. None was detected along the gentle gradient, although several factors did show more variability there than on the steep slope.

The abrupt distribution of the dominant species will in itself cause some discontinuity in the vegetation, if the vegetation is analyzed quantitatively. But there are other species whose change in density is correlated with the dominants, and these reinforce the discontinuity.

Among the more common shrubs and trees, at the transition from *Acacia* scrub to *Acacia senegal, Commiphora erythraea* disappears, *Grewia glandulosa* appears, and *Grewia villosa* is found on both sides. At the transition from *Acacia senegal* to *Acacia asak*, none disappear, but many species (*Acacia tortilis, Cissus rotundifolia, Cissus quadrangularis, Combretum aculeatum, Commiphora africana, Dichrostachys cinerea, Grewia bicolor, Grewia tembensis*) appear, and *Grewia villosa* and *Grewia glandulosa* are found on both sides. At the transition from *Acacia asak* to *Euphorbia candelabrum* woodland, *Cissus rotundifolia, Commiphora africana, Grewia bicolor, Grewia villosa, Ximenia americana* disappear; *Akocanthera schimperi, Carissa edulis, Euclea schimperi*, and *Rhus natalensis* appear; and several species are found on both sides—*Acacia tortilis, Cadia purpurea, Cissus quadrangularis, Dichrostachys cinerea*, and *Grewia glandulosa*. At the rapid transition (see Fig. 1) in the middle of the *Acacia asak* zone (1400 m), *Combretum aculeatum* disappears and *Cadia purpurea* appears.

In contrast to this, analysis of the gentle slope reveals very few changes of subdominant species simultaneous with changes in dominant species, except in the case of *Euphorbia candelabrum*. This species gradually becomes more common going up the gentle gradient, and two species, *Croton dichogamus* and *Psiadia arabica*, have nearly identical patterns to that of *Euphorbia*. No species disappear when *Euphorbia candelabrum* first appears, but several, including *Jasminum flori-*

bundum and *Lantana trifolia*, disappear when *E. candelabrum* becomes dominant.

The correlations of species limits along the steep slope may be brought about by direct biotic interactions—perhaps chemical interactions—or more commonly by sudden change in the physical environment caused by sudden change in species density. *Euphorbia candelabrum* has a very different physiognomy from other plants in this study, with its succulent, leafless, candelabra branches, and it also contains a poisonous latex, which may or may not affect the soil when branches of *Euphorbia* decay or when the leaves fall. It was the transition to *Euphorbia* woodland that caused the most sudden change along the steep slope (at about 1600 meters, Fig. 1), and even on the gentle slope vegetational change was most rapid as *Euphorbia candelabrum* increased in density (beginning at about 1700 meters, Fig. 1).

Another kind of physiognomic change that may affect the vegetation is illustrated by the fact that *Cadia purpurea* loses its leaves about 2 months earlier in the dry season than does *Calpurnia subdecandra*. This may have an effect on the understory plants. More subtle differences that change the physical environment (for example, differences in root systems) undoubtedly occur.

Conclusions

All of this indicates that along a steep gradient the vegetation itself can impose disjunctions on an extrinsically continuous environmental gradient, whereas along a gentle gradient it may not do so. Studies of several other slopes in Ethiopia, both gentle and steep, confirm the general differences shown by the two slopes of this study, but because of heterogeneity of environment—especially changes in bedrock—the results are not so clear-cut.

Other zoned communities, such as at a marine or lake shore, are also under the influence of a steep environmental gradient relative to the dispersal rate of the organisms. In many cases, vegetative reproduction plays an important role in these zonations, but in addition the competitive-exclusion principle is probably influential in demarcating plant communities, as defined by the dominant species, along a rapidly changing environmental gradient. There is no reason for saying that such discrete communities are more nearly normal, or less so, than the vegetational continuums found in other situations.

In fact, portions of the steep altitudinal gradient of this study do show continuous vegetational change. Some of the "zone" can hardly be considered a single community. The transitions from communities dominated by *Acacia venosa* to those dominated by *Acacia mellifera* to those dominated by *Acacia senegal* are continuous. The *Acacia asak* zone has a different composition at its lower and upper limits—*Cissus rotundifolia, Combretum aculeatum, Grewia bicolor, Grewia tembensis*, and *Grewia villosa* are more abundant in the lower part of the zone; *Cadia purpurea, Grewia glandulosa*, and *Ximenia americana* are more abundant in the upper part. The *Euphorbia* woodland has almost completely different shrub layers at the lower (dominated by *Akocanthera schimperi* and *Cadia purpurea*), middle (dominated by *Calpurnia subdecandra, Dodonaea viscosa, Euclea schimperi*), and upper levels (dominated by *Carissa edulis* and *Rhus natalensis*), though the change from one to the next is continuous.

The question that should bother ecologists is not really whether vegetation forms a continuum or forms natural and discrete groupings. It is obviously capable of forming both. Even Daubenmire (*1*) concedes that on the basis of "species distribution and relative abundance over the landscape, vegetation is a continuum." (He believes that these are not the most important characteristics of a community, and that on the basis of "population structure and dynamics" typal communities can be found.)

The question that should be asked is, What methods should be used in the analysis of vegetation—a continuum approach or a classificatory approach? Despite Daubenmire's view (*17*) that the two approaches are "strictly incompatible," and that "without classification there can be no science of vegetation," the methods to be used depend on the objectives. Continuum or gradient analysis can detect discontinuities in the vegetation, whereas a classificatory system cannot detect continuities. For purposes of mapping or landscape inventory, classification is necessary and informative; for understanding the sociology of plant communities, some kind of gradient analysis, such as the simple one used here, appears to be more efficient.

Summary

A comparison of steep and gentle slopes in a semiarid part of Ethiopia revealed that there was more discontinuity in the vegetational change caused by altitude along the steep slope than along the gentle slope. The vegetation on both slopes ranged from subdesert *Acacia* scrub to succulent *Euphorbia* woodland. The shape of distribution curves of individual species along the altitudinal gradient showed differences between the two slopes. In contrast to the nearly bell-shaped curves along the gentle gradient, the distribution patterns along the steep gradient tended to be flat-topped and steep-sided. This type of pattern was most pronounced in species exhibiting dominance in the community. Along the steep slope the principle of competitive exclusion may be more influential than along the gentle slope. Therefore under certain conditions, a portion of the vegetation can develop discontinuity despite a continuous environmental gradient. Between the major discontinuities however, there can be continuous vegetational change. The gentle slope showed continuous vegetational change along the entire length of the environmental gradient studied.

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